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LIFE HISTORY AND IMMATURE STAGES OF TWO SPECIES OF *MEGASELIA* (DIPTERA: PHORIDAE) PREDATORY ON GALL-INHABITING INSECTS

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Abstract.—Larvae of *Megaselia chainensis* are predators of the cockscomb leaf gall aphid *Colopha ulmicola* on elm trees. Larvae of *M. submarginalis* are predators of larval *Contarinia negundifolia,* a leaf gall-inducing cecidomyiid fly on boxelder trees. Larvae of both *Megaselia* species consume several hosts during their development. Both are univoltine and synchronized with the life cycles of their hosts. Larvae of both species are described and illustrated.

Key Words: Aphidae, Cecidomyiidae, gall, *Megaselia,* natural history, Phoridae, predator

The usual representation of phorid flies as indiscriminate scavengers is incorrect. We know of a large variety of life histories in this family, including those of species that are herbivores, predators, and parasitoids attacking a diverse array of prey and hosts (Schmitz 1938, Disney 1990). Recently, Ferrar (1987), Disney (1983) and Kistner (1982) have summarized information on predatory and parasitoid phorid species.

The purpose of this paper is to publish data on two further predatory species of *Megaselia* Rondani, one that attacks larvae of a species of cecidomyiid fly (Diptera: Cecidomyiidae) and one that attacks immatures and adults of an aphid species (Homoptera: Aphidae) (Robinson 1970). Other phorids are known to attack Diptera larvae, for instance larvae of *M. flavicoxa* Zetterstedt and *M. obscuripennis* (Wood) are parasitoids of sciarid larvae, larvae of *Peromitra incrassata* (Meigen) are endoparasites of larval *Bibio marci* (Linnaeus) (Diptera: Bibionidae) (Morris 1922, Gemesi and Disney 1991), larvae of *P. germanica* (Schmitz) are parasitoids of *Penthretia holosericea* Meigen (Diptera: Bibionidae) (Gemesi and Disney 1991), larvae of *M. mallochi* (Wood) are predators of sciarid pupae (Krespi et al. 1985, Deleporte 1986) and *M. paludosa* larvae are true parasites in tipulid larvae (Disney 1983). Our record of *M. submarginalis* (Malloch), however, seems to be the first example of a true predator of Diptera larvae, that is, one which kills many hosts. Other than *M. chainensis,* the only phorid species that has been recorded as attacking aphids is *Phora holosericea* Schmitz, whose larvae eat root aphids on various plants (Yarkulov 1972).

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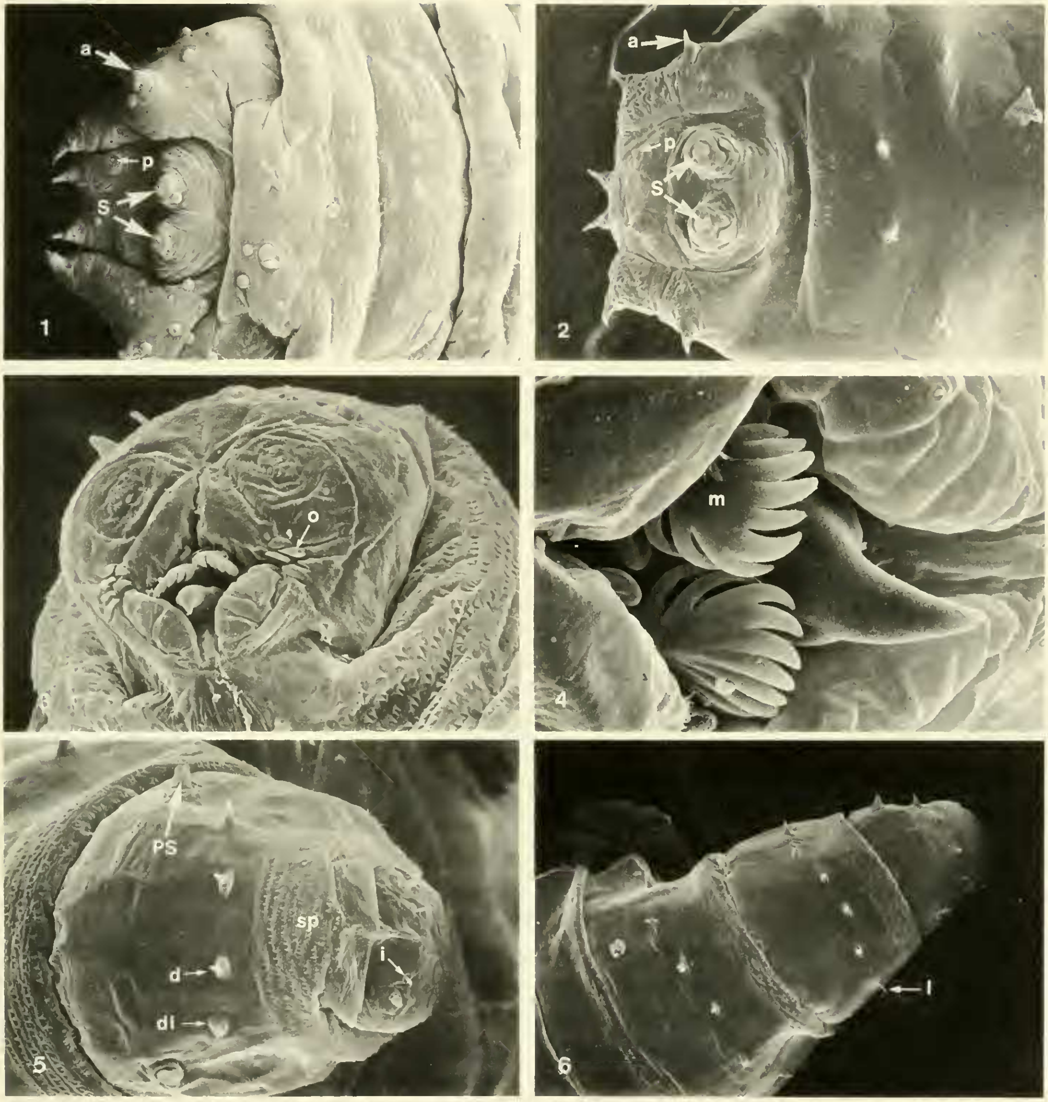


Figs. 1–6. Larvae of *Megaselia* species. 1, *M. submarginalis,* terminal segments, dorsal; Figs. 2–6. *M. chainensis.* 2, terminal segments, dorsal; 3, cephalic segment, ventral; 4, oral region; 5, cephalic segment and prothorax, dorsal; 6, thorax, dorsal. Abbreviations: a—anterior lateral papilla, d—dorsal papilla, dl—dorsolateral papilla, i—interantennal papilla, l—lateral papilla, m—mandible, o—oral papillae, p—posterior spiracular papilla, ps—prothoracic spiracle, s—terminal spiracle, sp—spinulae.

METHODS AND MATERIALS

Life history observations and photographs of larvae and prey of *M. chainensis* and *M. submarginalis* were provided by the senior author. Illustrations and descriptions of immature stages, and discussion of relationships were provided by the junior author.

Specimens were handled and examined as follows: larvae brought into the laboratory were reared in petri plates and provided with food and moist filter paper as a substrate. Larvae were collected into alcohol, sonicated in alcohol and ammonium hydroxide, critical-point-dried, sputter coated with gold-palladium, and examined with a Cambridge Stereoscan 100.

DESCRIPTION OF TAXA

Megaselia chainensis **Disney 1985**

Plastophora subconvexa Borgmeier 1963
Megaselia subconvexa, Disney 1978

(Figs. 2–13, 19–22)

Third-instar larva

Head.—Interantennal papilla present, level with antenna (Fig. 5, i). Several small papillae present lateral to oral opening (Fig. 3, o). Basal portion of dorsal and ventral cornua of cephalopharyngeal skeleton darkly sclerotized; ventral cornu elongate, enlarged, much longer than dorsal cornu, mostly unsclerotized (Fig. 13). Hypopharyngeal skeleton separated from cornua. Labium short. Mandible with numerous, medially-curved teeth (Figs, 4, m, 13, m; also Sinclair 1992, fig. 28). Parastomal bars thin. Pharyngeal ridges distinctly visible.

Thorax.—Each segment encircled by anterior rows of spinuli (Fig. 5, sp). Prothorax with dorsal (Fig. 5, d) and dorsolateral (Fig. 5, dl) papilla, anterior to spiracle (Fig. 5, ps). Spiracle apically bilobate. Mesothorax and metathorax with dorsal, dorsolateral and lateral (Fig. 6, l) papilla. Each segment with small, ventral creeping welt with small papillae (Fig. 7).

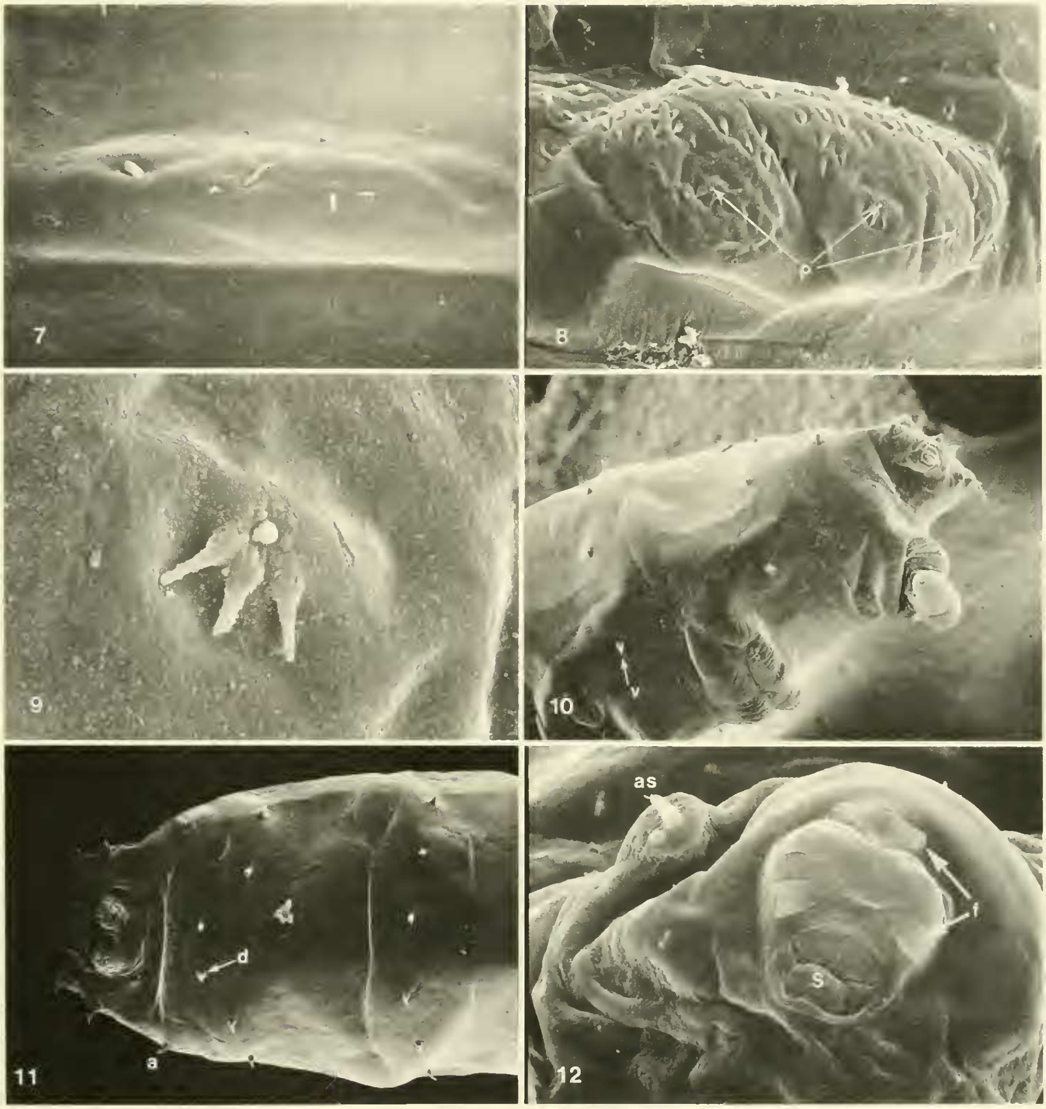
Abdomen.—Segments 1–6 with same six papillae found on mesothorax and metathorax, plus one ventral papilla (Fig. 10, v); all found along posterior one-third; segment 7 with all except dorsal, most medial (Fig. 11, d) anteriorly displaced; segment 8 with large, anterior papilla (Fig. 11, a), two large, lateral papillae and one small posterior papilla (Fig. 2); one papilla anterior (Fig. 12, as) and one posterior (Fig. 2, p) to spiracle. Flattened spiracular processes (Fig. 12, f) present beside posterior spiracle; four spiracular slits present. Ecdysial scar large, prominent (Fig. 12, s). Ventral creeping welt with three small papillae (Fig. 8, p), each surrounded by rosette of processes (Fig. 9).

Life history.—In the spring and early summer, aphids of the species *Colopha ulmicola* Fitch induce cockscomb galls on the leaves of American elm trees (*Ulmus americana* L.). These galls, each with several aphids, apparently are a natural oviposition site for *M. chainensis.* Field and laboratory observations indicate that the female phorid deposits 1–3 eggs within a gall (Fig. 21, e). No eggs were found outside galls. The female oviposits through the slit-like opening of the gall on the underside of the leaf (Fig. 19), and apparently does not discriminate between galls that contain aphids (Fig. 20, a), and those that are empty or damaged.

Soon after hatching, the first-instar larva begins feeding on the aphids within the gall. Its behavior is similar to that of the second- and third-instar larvae. The larva attacks an aphid by rasping at the integument with its mouth hooks. Once an opening is made in the integument, the larva eats the internal contents of the aphid. The second-instar larva remains in the gall and continues to feed on the enclosed aphids. If several larvae are in one gall, the number of aphids available for food diminishes, and some larvae leave the gall through the opening of the underside of the leaf. The third-instar larva continues to feed on aphids, including the spring migrant (alate) forms that are developing in the gall. The mature third-instar larva remains in the gall and pupariates.

The pupal respiratory horns appear after about 72 h, and after one month an adult is formed within the puparium (Fig. 22, p). The adult remains in this state until the following spring. There are one or perhaps two generations per year.

Geographic distribution.—Widespread in Canada and the northern United States of America (Borgmeier 1963, Robinson 1970).

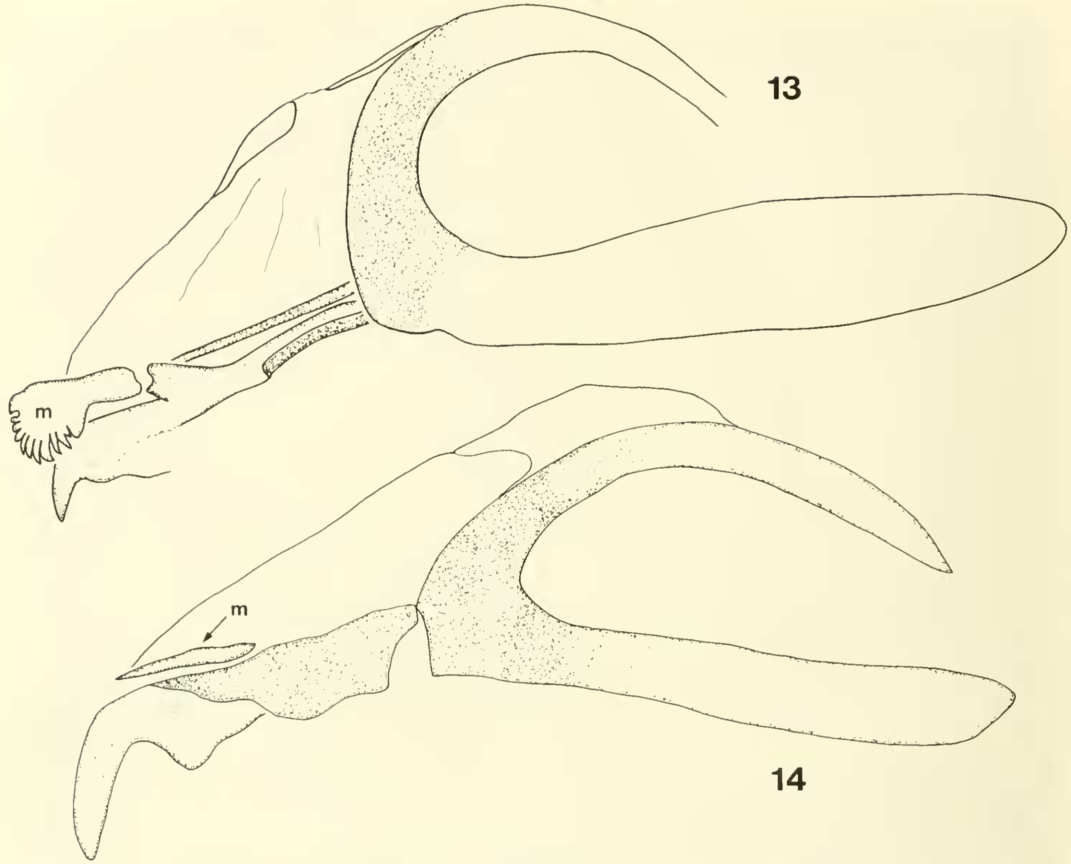


Figs. 7–12. Larva of *M. chainensis.* 7, mesothoracic creeping welt, ventral; 8, abdominal creeping welt, ventral; 9, papilla of abdominal creeping welt; 10, terminal segments, lateral; 11, terminal segments, dorsal; 12, spiracular region, dorsal. Abbreviations: a—anterior papilla of segment 8, as—anterior spiracular papillae, d—dorsal papilla, f—flattened spiracular process, p—papillae, s—ecdysial scar, v—ventral papilla.

Megaselia submarginalis **(Malloch)**
Aphiochaeta submarginalis
Malloch 1912
Megaselia (*Aphiochaeta*)
submarginalis, Brues 1950,
Borgmeier 1964
Plastophora submarginalis,
Borgmeier 1966
Megaselia submarginalis,
Disney 1978
(Figs. 1, 14–18)

Third-instar larva

The few available specimens of this species were killed and preserved in alcohol almost thirty years ago, and they have de-



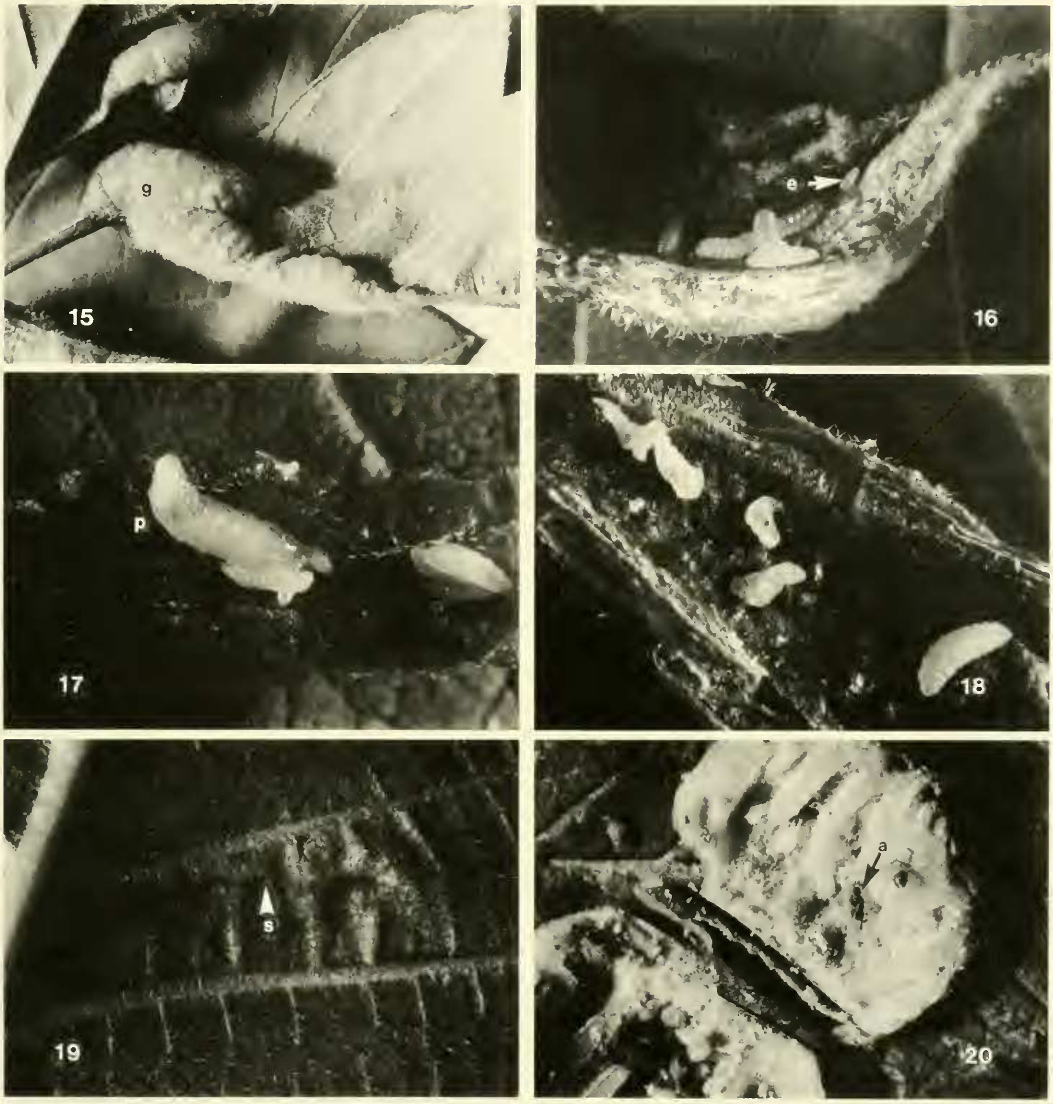
Figs. 13, 14. Cephalopharyngeal skeleton, lateral. 13, *M. chainensis*; 14, *M. submarginalis*. Abbreviation: m—mandible.

composed substantially, making it difficult to produce SEM illustrations of publishable quality. In general, papillae and body form are similar to those of *M. chainensis.* The following are some features of the larva of *M. submarginalis* that might be useful for distinguishing it from that of *M. chainensis*:

Cephalopharyngeal skeleton (Fig. 14). Bases, but not apices, of cornua darkly sclerotized. Labium elongate. Hypopharyngeal skeleton markedly separated from cornua. Mandible thin, elongate, not toothed (Fig. 14, m). Pharyngeal ridges faint.

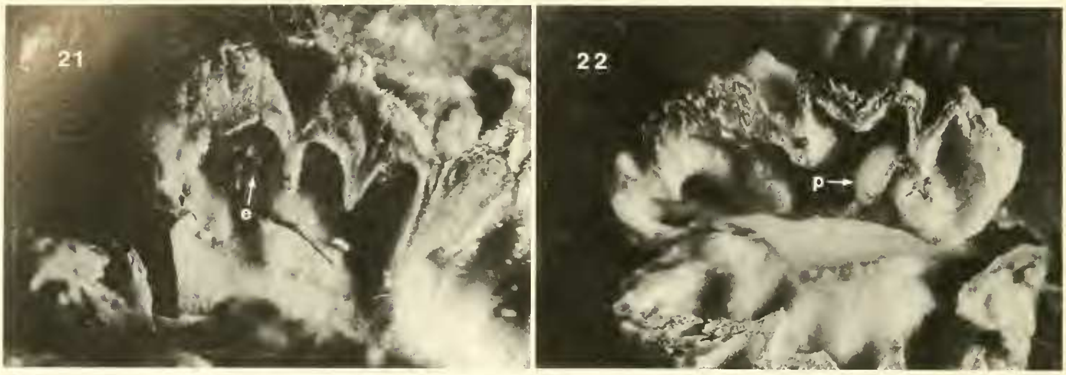
Abdominal segment 8 (Fig. 1). Most anterior lateral papilla (Fig. 1, a) small; posterior lateral papilla directed posteriorly; post-spiracular papilla (Fig. 1, p) smaller than that of *M. chainensis* (compare with Fig. 2, p).

Life history.—During early- to mid-May, larvae of the cecidomyiid fly, *Contarinia negundifolia* Felt, induce galls (Fig. 15, g) on the leaves of boxelder trees, *Acer negundo* L. (Wilson 1966). These galls, each with several cecidomyiid larvae (Fig. 16), apparently are a natural oviposition site for *M. submarginalis.* Field and laboratory observations indicate that the female deposits one egg within a gall (Fig. 16, e), after inserting the tip of her ovipositor into the upper opening of the gall, generally near the apex of the leaf. Eggs were not found outside the gall, and only one egg or larva was found in each infested gall.



Figs. 15–20. Life history and microhabitat of *Megaselia* species. Figs. 15–18. *M. submarginalis*. 15, boxelder leaf gall; 16, larvae of *Contarinia negundifolia* and egg of *M. submarginalis*; 17, larva of *M. submarginalis*; 18, four consumed and one living larva of *C. negundifolia*; Figs. 19, 20. *M. chainensis*. 19, ventral slit in elm cockscomb gall; 20, cockscomb gall opened to expose aphids. Abbreviations: a—aphid, e—egg, g—gall, p—phorid larva.

Soon after hatching, the first-instar phorid larva begins feeding on a cecidomyiid larva. The feeding behavior of the first-instar larva is similar to that of the second and third instar larvae. It curls around the cecidomyiid larva and begins rasping at the integument with its mouth hooks. Once an opening is made in the integument, the phorid larva consumes the internal contents of the cecidomyiid. The second-instar larva remains in the gall and continues to eat the enclosed cecidomyiid larvae. Three to six cecidomyiid larvae are consumed during this period, but the contents of each prey item



Figs. 21, 22. Life history of *M. chainensis.* 21, phorid egg in exposed cockscomb gall; 22, phorid puparium in exposed cockscomb gall. Abbreviations: e—egg, p—puparium.

are not always completely ingested. Several partially consumed cecidomyiid larvae can be found in most infested galls (Fig. 18). During the third stadium, the phorid larva continues to eat cecidomyiid larvae (Fig. 17, p), and apparently it completes development in a single gall. No phorid larvae were seen outside of galls until development was completed; thereafter they dropped to the ground where they pupariate.

After approximately 72 h the pupal respiratory horns appear. After one month, an adult is formed within the puparium, where it remains until the following spring. The life cycle of the phorid is correlated with that of its univoltine prey, as there is one generation per year.

Geographic distribution.—Widespread in Canada and the northern United States of America (Robinson 1970).

TAXONOMIC AND PHYLOGENETIC NOTES

The species of *Megaselia* discussed in this paper were formerly classified in the genus *Plastophora* Brues, which Disney (1978, 1986) subsequently reduced to a synonym. Previously, species of *Plastophora* were characterized by females with a sclerotized ovipositor, but the degree of sclerotization varied widely among species, and these two species are among those with the least sclerotized ovipositors. They probably do not belong in a monophyletic group with many of the other species formerly classified as *Plastophora,* now classified in *Myriophora* Brown (Brown 1992). The genus *Megaselia* itself has been shown to be a paraphyletic group with respect to some other genera within the phorid subfamily Metopininae (Disney 1989), and will eventually have to be organized into monophyletic units.

DIVERSITY OF *MEGASELIA*

Approximately 1200 species of phorid flies were classified in the genus *Megaselia* at the time the catalogue of world Phoridae was published (Borgmeier 1968). Life histories of most species are completely unknown, but recent studies have shown that many are predators and parasitoids, restricted to one or a few hosts. This marked host specificity apparently allows the within-site diversity of *Megaselia* to be extremely high, often exceeding 50 species (Disney 1987, Brown 1989).

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